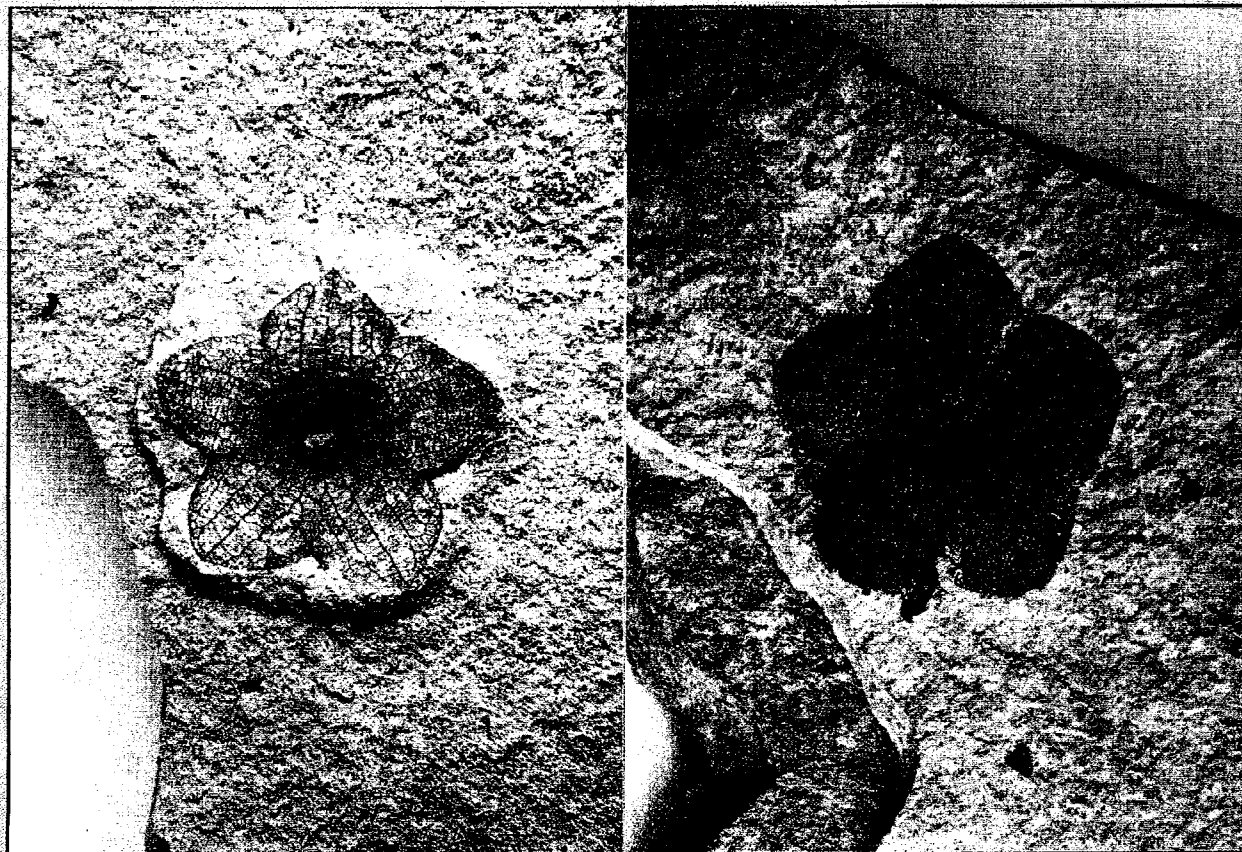


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FLOWERS, FRUITS, AND POLLEN OF FLORISSANTIA, AN EXTINCT MALVALEAN GENUS FROM THE EOCENE AND OLIGOCENE OF WESTERN NORTH AMERICA¹

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Compressed flowers and fruits of *Florissantia* (Lesquereux) comb. nov. from the latest Eocene of Colorado and Montana and from the middle Eocene to early Oligocene of Oregon were reinvestigated using the type material and more recently collected specimens. Two additional species, *Florissantia quilchenensis* (Mathewes & Brooke) comb. nov. from the middle Eocene of British Columbia and Washington and *F. ashwillii* sp. nov. from the middle Eocene to early Oligocene of Oregon, are also recognized on the basis of differences in perianth and anther morphology. *Florissantia* flowers are borne on long (up to 3 cm) pedicels and possess a large (2.3–5.3 cm diam), shallowly campanulate, five-lobed, persistent gamosepalous calyx. The fertile parts include a superior, pentagonal ovary, a single style with five stigmas, and a cycle of five stamens with bifurcate filaments topped by stout anthers or half anthers. Pollen removed from the anthers is oblate, 20–32 μ m equatorial diam, 3(–4)-colporate, with short colpi and reticulate ornamentation. Although formerly placed in *Porana* (Convolvulaceae) and *Holmskioldia* (Verbenaceae), the newly recognized characters of floral and pollen morphology demonstrate that the genus belongs within the Malvales as an extinct genus possessing features found today in Tiliaceae, Bombacaceae, and Sterculiaceae. Recognizing that there is much overlap among extant genera of these families, and that the circumscription of these families is in need of systematic revision, the fossil is tentatively placed in the Sterculiaceae. *Florissantia* flowers exhibit a syndrome of features suggestive of insect or bird pollination, while the fruits, provided with a large, persistent, membranous calyx, appear to be well adapted for wind dispersal. Dismissal of this and other purported verbenaceous fossils from the Verbenaceae casts doubt on the presence of Verbenaceae in the early Tertiary of North America.

The Sterculiaceae, Tiliaceae, Bombacaceae, and Malvaceae form a natural group within the Malvales linked by similarities of floral morphology (van Heel, 1966), pollen morphology (Erdtman, 1952, p. 78), wood anatomy (Metcalfe and Chalk, 1950; Manchester and Miller, 1978), and leaf architecture (Wolfe, 1989, p. 95). As traditionally defined, these families overlap in many characters, and the criteria on which they are distinguished from one another have been regarded as weak in some instances (Hutchinson, 1967). As currently circumscribed, these families are probably paraphyletic, and the need for modern systematic revision has impeded the understanding of paleobotanical data. Nevertheless, the Malvales have an excellent fossil record, and paleobotanical data may help in clarifying the evolution of this systematically diverse group.

The evolutionary radiation of core malvalean families, including the Sterculiaceae, Tiliaceae, Bombacaceae, and Malvaceae, appears to have been a latest Cretaceous to early Tertiary phenomenon, judging from the fossil records of the distinctive wood (Manchester, 1979, 1980; Wheeler, Lee, and Matten, 1987) and dispersed pollen (Mai, 1961; Krüttsch, 1970; Muller, 1981). *Tilia* is first recognized on the basis of leaves from the middle Eocene

(Wolfe and Wehr, 1987) and is confirmed on the basis of distinctive fruiting bracts from the late Eocene and early Oligocene (Hall and Swain, 1971; Manchester and Meyer, 1987; Manchester, 1991). Fossil fruits formerly called *Pteleacarpum* Weyland, which were widespread in the Tertiary of the Northern Hemisphere (Bůžek, Kvaček, and Manchester, 1989), have recently been identified as belonging to the extant Chinese tiliaceous genus *Craigia* (Kvaček, Bůžek, and Manchester, 1991). Saporta (1862, 1873) described and illustrated probable bombacaceous flowers with intact stamens under the name *Bombax sepulchrum* from the Oligocene of Gypses, Aix-en-Provence, France (Muséum National d'Histoire Naturelle, Paris no. 14745). Mai (1961) described an extinct Tiliaceous genus, *Burretia*, based on a flower bearing pollen of the *Intratropipollenites instructus* (R. Pot.) Pfl. & Th. type from the Pliocene of Germany. Aside from these reports, the fossil record of flowers and fruits corresponding to the Malvales is largely unknown.

This paper presents a newly recognized extinct malvalean genus from the Eocene and Oligocene of western North America. Known as *Florissantia* (Knowlton, 1916), the compressed flowers and fruits are a conspicuous element of middle Eocene to early Oligocene lake deposits in Colorado, Wyoming, Utah, Montana, Oregon, Washington, and British Columbia. The first known example was described by Lesquereux (1883) from the Florissant beds of Colorado and attributed to the convolvulaceous genus *Porana*. In his monographic study of the Florissant flora, MacGinitie (1953) provided a synonymy of other published records, documented new specimens from Florissant, and reassigned the flower to the extant verbenaceous genus *Holmskioldia*. The resulting name, *Holmskioldia speirii* (Lesq.) MacGinitie, has become ingrained in the paleobotanical literature over the past few decades (Brown, 1959; Becker, 1961; Meyer, 1973; Taylor, 1990).

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However, this taxonomic determination was based on limited morphological information, chiefly the shape and venation of the calyx. The lack of data concerning the gynoecium and androecium precluded a well-informed determination of affinities.

Larger collections made during the past decade, including especially well-preserved specimens from the lower Oligocene John Day Formation of Oregon and from the middle Eocene Republic flora of Washington, provide a wealth of new characters pertaining to the gynoecium, androecium, and pollen of *Florissantia*. Combined data from flower, fruit, and pollen morphology indicate that the flowers do not belong to any of the previously suggested families but, rather, represent an extinct genus of malvalean affinity.

The purposes of this paper are to: 1) document the floral (including pollen) morphological characters of the three recognized species (*F. speirii*, *F. quilchenensis*, and *F. ashwillii*); 2) assess the systematic affinities within the Malvales; 3) discuss the pollination and dispersal ecology, evolutionary considerations, and distribution; and 4) challenge the reported fossil history of Verbenaceae in the Tertiary of North America.

MATERIALS AND METHODS

The flowers and fruits are preserved as impressions and compressions in shale, so that their original three-dimensional morphology must be inferred from specimens that have been flattened in various orientations. After the initial exposure of the fossil by splitting of the shale, microexcavation of successive layers of the rock with fine needles under a dissection microscope was sometimes successful in revealing structures such as the fruit body and stamens hidden within the sediment.

The holotype of *Porana speirii* Lesquereux, and other topotypic material from the Florissant flora of Colorado, were examined at the U.S. National Museum, Washington, D.C. (USNM). Additional specimens from Florissant were studied at collections of the University of California Museum of Paleontology, Berkeley (UCMP), the University of Washington, Seattle (UW), and the Florida Museum of Natural History, University of Florida, Gainesville (UF). This material furnishes excellent details of perianth morphology and provides the basis for identifying material from other regions; however, none of the specimens currently available from the Florissant flora clearly shows the organization of the gynoecium and androecium. A radiometric date of 34.8 million years (MY) for the Florissant Tuff (Epis and Chapin, 1974; corrected to new constant) indicates that this locality is very near the Eocene/Oligocene boundary, which is currently placed at 34.0 MY (Swisher and Prothero, 1990).

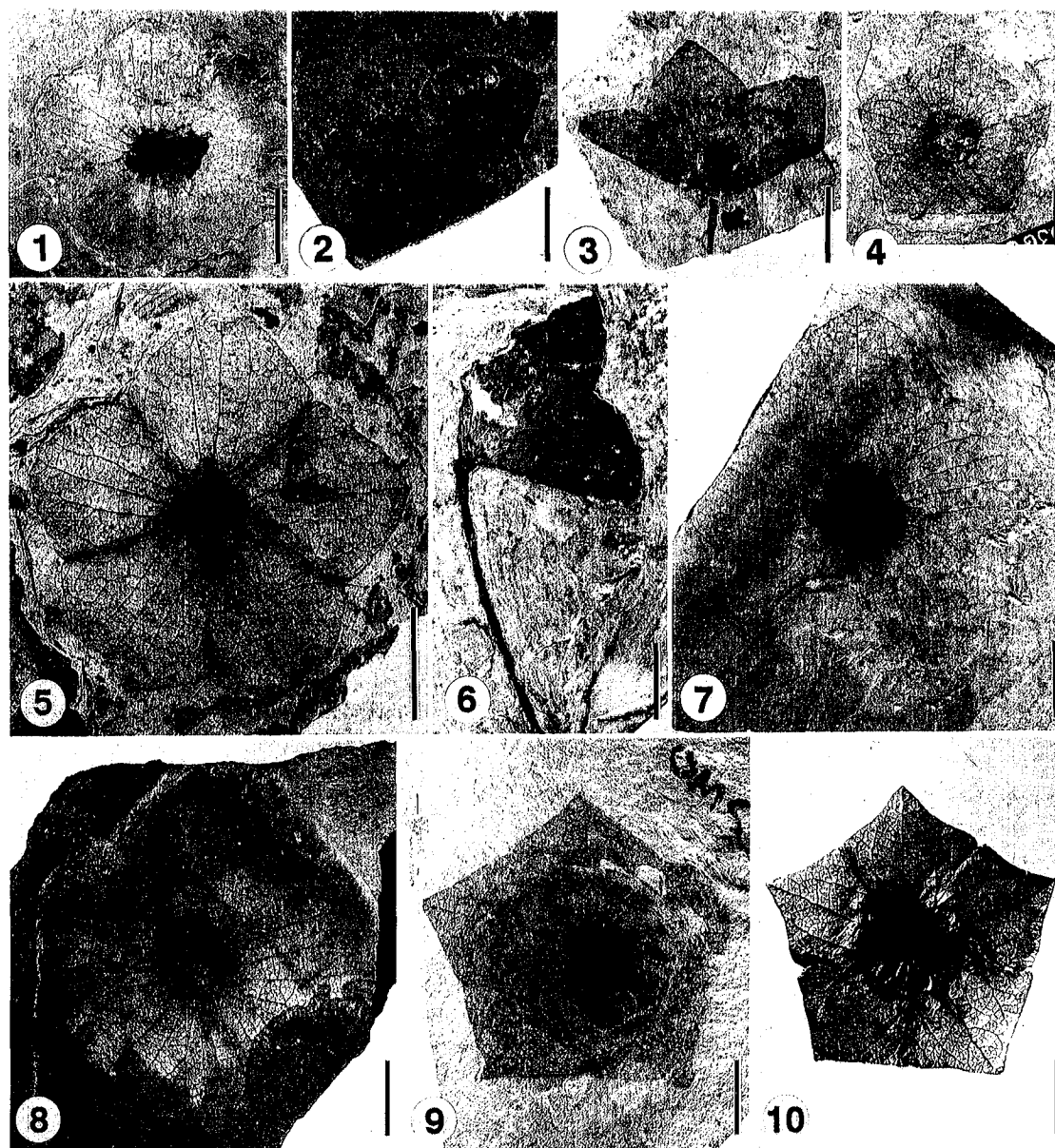
The most informative specimens of *Florissantia speirii*, including those with intact fertile parts, were collected from lower Oligocene localities of the Bridge Creek flora of the John Day Formation in north central Oregon and are deposited in the paleobotanical collections of UF and UCMP. The Bridge Creek localities include Wheeler High School, Dugout Gulch, Knox Ranch, Allen Ranch, Gray Ranch, and Lost Creek Reservoir (Manchester and Meyer, 1987; Manchester, 1990). Although several specimens of *F. speirii* show stamens, only two specimens (Figs. 15,

18) have pollen preserved in the anthers. These two were collected in 1987 and 1988 from a thin layer of relatively unoxidized, brown sediment near the top of the stratigraphic section of shales at Wheeler High School in Fossil, Oregon. This locality has been dated at 32.1 ± 0.69 MY, based on argon 40/39 analyses of ten plagioclase crystals removed directly from the fossiliferous tuff (Turrin, in Manchester, 1990). The other John Day localities are also believed to be about 32 MY old, based on their stratigraphic position relative to adjacent radiometrically dated rocks (Manchester, 1990). Still older examples of *F. speirii* were collected from middle Eocene localities of the Clarno Formation in north central Oregon (West Branch Creek, Horseheaven, Gosner Road, and White Cliffs). These localities are floristically similar to each other and are probably similar in age. An argon 40/39 date of about 44.7 MY was obtained based on plagioclase crystals isolated from the interbedded tuff at the White Cliffs locality (Manchester, 1990).

The type material of *Florissantia quilchenensis* from the Eocene of Quilchena, British Columbia (Mathewes and Brooke, 1971) was borrowed from Simon Fraser University (SFU) through the courtesy of R. Mathewes. Numerous specimens of the same species were examined from the Republic flora of northeastern Washington through the courtesy of Wesley Wehr, Burke Museum, University of Washington, Seattle (UWBM), and Stone-rose Interpretive Center, Republic, Washington (SR). The Republic flora is considered to be of middle Eocene age (Wolfe and Wehr, 1987).

Many well-preserved specimens of *Florissantia ashwillii* sp. nov., including the holotype, were collected from the Sheep Rock Creek locality in central Oregon (Manchester, 1990). Although this pond deposit is isolated from strata suitable for radiometric dating, the presence of a palm leaf fragment suggests that it belongs to the Clarno Formation and is consistent with middle or late Eocene age. Numerous additional specimens were collected from the Sumner Spring localities on Gray Butte (Ashwill, 1983; McFadden, 1986). The Sumner Spring shales probably belong to the John Day Formation and are probably lower Oligocene. Specimens from the lower Oligocene Goshen flora of Oregon (Chaney and Sanborn, 1933) were borrowed for study from UCMP and UWBM.

Masses of pollen were retrieved from the fossil stamens by processing fragments of carbonaceous material removed from the anthers. The fragments were cleaned in hydrofluoric acid and macerated in a drop of concentrated nitric acid, washed in water, then cleared with a drop of ammonia. After washing and dehydration, the pollen residue was: 1) mounted on microscope slides with Canada balsam or glycerine jelly for light microscopy; 2) evaporated onto aluminum stubs for scanning electron microscopy (SEM); and 3) embedded in Epon, sectioned, and stained with uranyl acetate and lead citrate for transmission electron microscopy (TEM). SEM analysis was performed on a Hitachi Field Emission scope, courtesy of G. Erdos, at the UF Interdisciplinary Center for Biotechnology Research Electron Microscopy Core Laboratory. TEM sections were prepared and examined at 80 kV in a JEOL 2000FX scope, courtesy of C. Daghljan, at the Rippel Electron Microscope Facility, Dartmouth College.



Figs. 1–10. *Florissantia speirii* (Lesquereux) comb. nov. from Colorado and Oregon. 1. Holotype of Lesquereux 1883, showing typical transversely compressed calyx with rounded lobes and shallow sinuses, USNM 387553, $\times 1$. 2. Specimen showing transversely compressed calyx and laterally compressed ovate gynoecium, USNM 34236, $\times 1$. 3. Laterally compressed flower showing dark elliptical outline of the ovary, prominent calyx, and pedicel, USNM 332406, $\times 1$. 4. Transversely compressed calyx showing pentagonal outline, original specimen of *Florissantia physalis* Knowlton 1916, USNM 33685, $\times 1$. 5. Transversely compressed calyx enlarged to show typical venation, UF 9982, $\times 1.5$. 6. Laterally compressed flower showing typical long pedicel, UF 10409, $\times 1$. 7. Large calyx showing concentric circular outlines of the androgynophore and fruit body impression (cf. Fig. 21), UF 7031, $\times 1$. 8. Calyx with portion of fruit body exposed in the center, UF 11703, $\times 1$. 9. Pentagonal calyx with poorly developed sinuses between lobes, UF 11704a, $\times 1$. 10. Extant *Schoutenia accrescens* (Mast.) Merr., Sungai Sedili, Johore, Malaya Penn., A: Ngadiman 36846. Localities: 1–5. Late Eocene Florissant beds, Colorado. 6. Early Oligocene John Day Formation, Dugout Gulch, Oregon. 7. Early Oligocene John Day Formation, Fossil, Oregon. 8, 9. Middle Eocene Clarno Formation, West Branch Creek, Oregon. Bars = 10 mm in Figs. 1–3, 5–10, and 7 mm in Fig. 4.

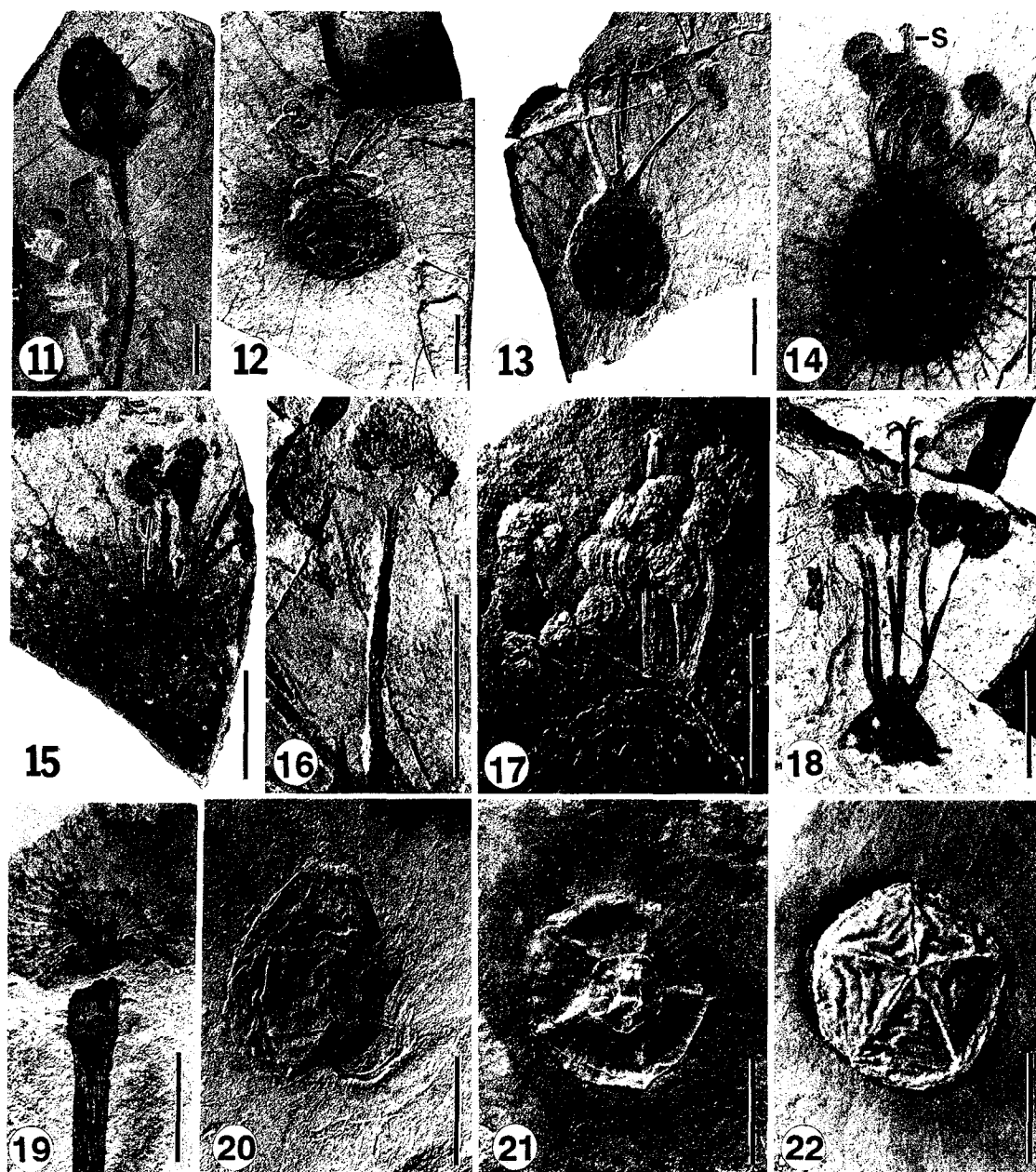
SYSTEMATICS

Florissantia Knowlton emend.—Figs. 1–9, 11–53.

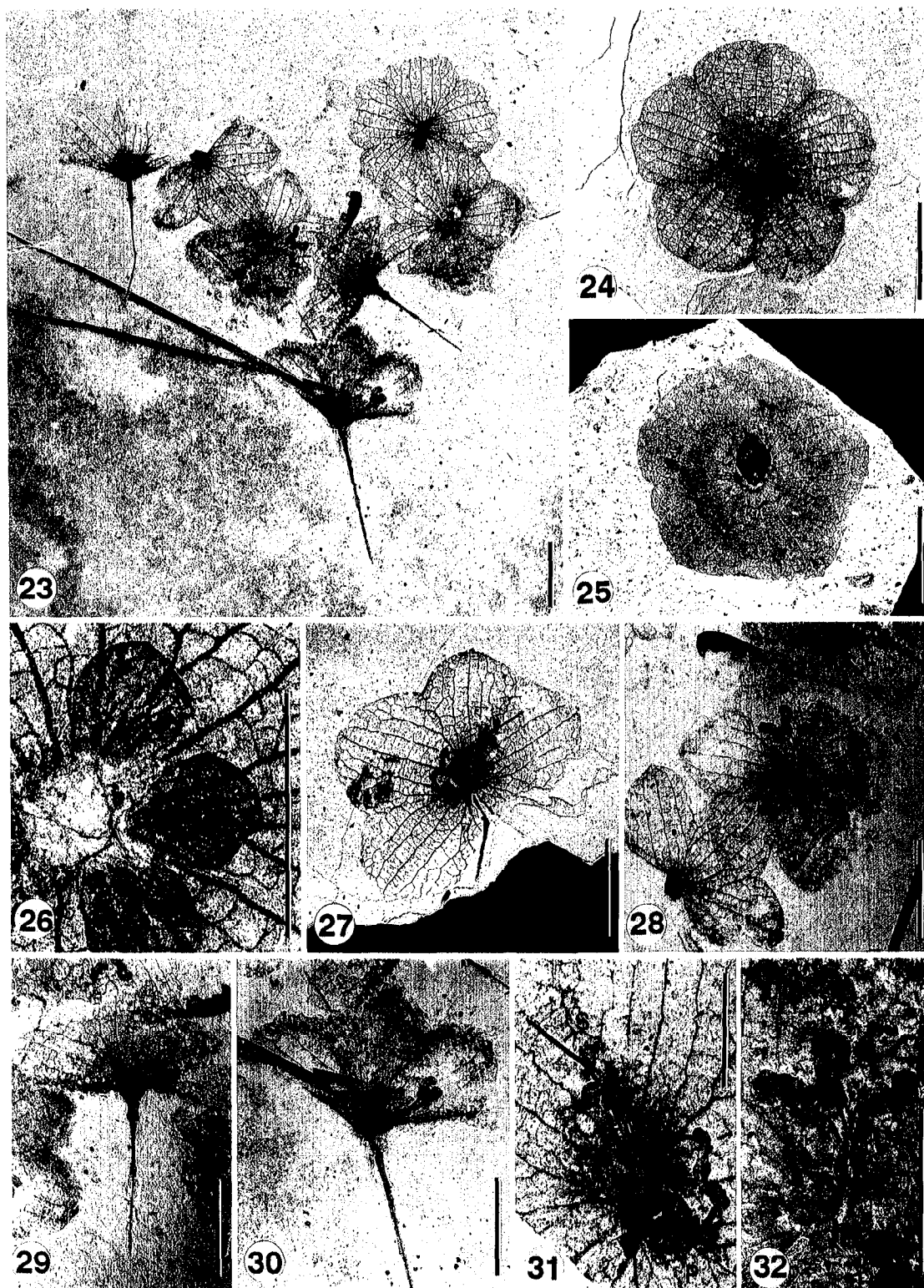
Type—*Florissantia physalis* Knowlton 1916, p. 270 = *Florissantia speirii* (Lesquereux) Manchester (based on *Porana speirii* Lesquereux 1883).

Emended generic diagnosis—Relatively large (> 20 mm diam), actinomorphic flowers borne on long pedicels. Calyx shallowly campanulate, membranaceous, with five sepals fused at least 50% of their length, with prominent,

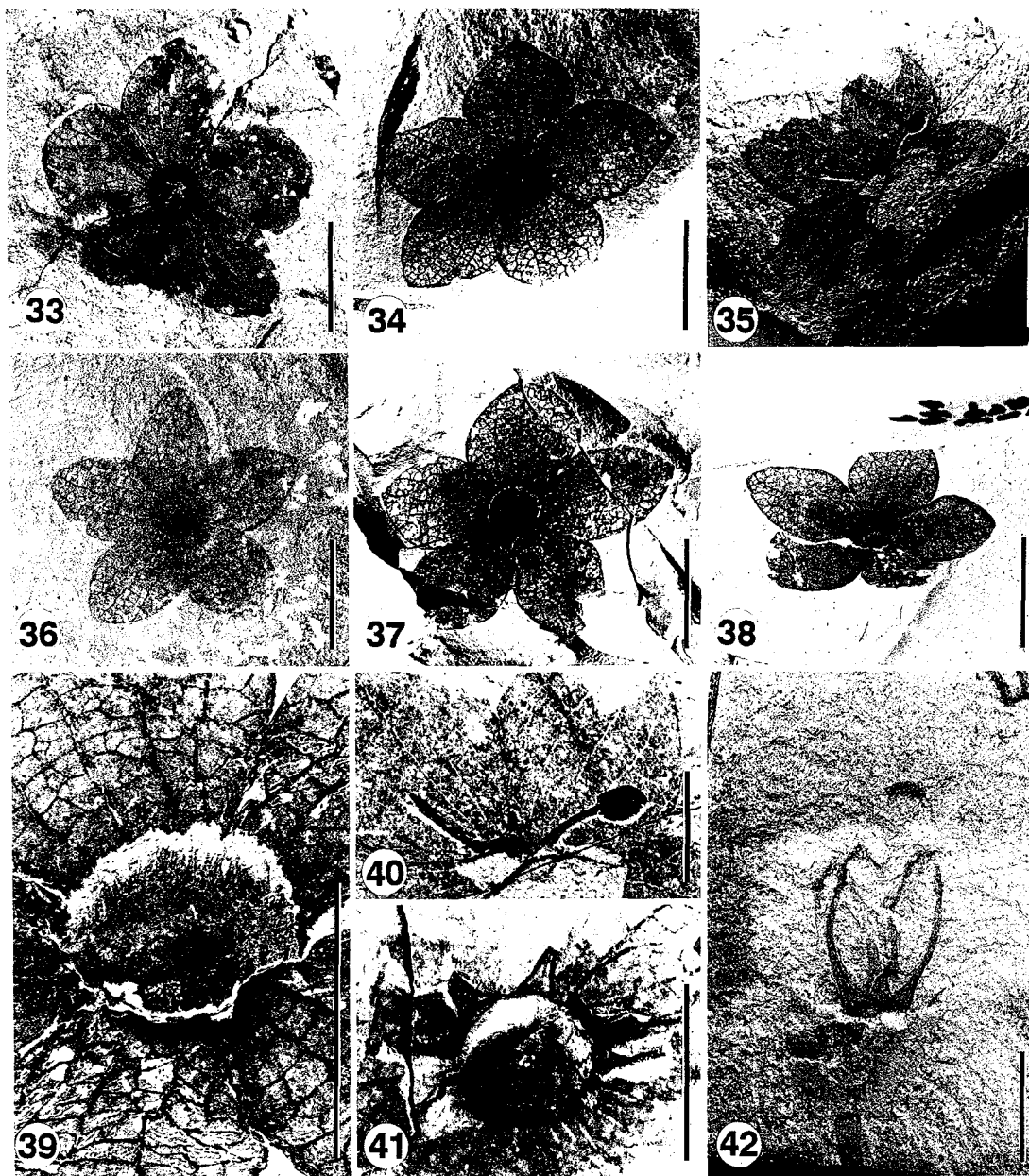
radiating reticulate venation. Each sepal with five to seven veins diverging from the base and pursuing a straight course to the margin, where they unite by anastomosing loops; a prominent vein leading to points of sinuses and giving off a few lateral branches; veins joined by lateral crossveins, forming a conspicuous network of irregularly polygonal or rectangular meshes. Calyx tissue thicker, and/or densely hairy near the base. Corolla absent (two species) or present (one species), consisting of five free, thick petals smaller than the sepals in fully developed



Figs. 11–22. Details of the gynoecium and androecium of *Florissantia speirii* from the lower Oligocene John Day Formation, north central Oregon. 11. Laterally compressed elliptical fruit body on long pedicel with remains of calyx and stamens, Dugout Gulch, OR, UF 10410, $\times 1.4$. 12. Specimen showing venation of calyx, pentagonal outline of the transversely compressed fruit, and the laterally compressed persistent androecium with thick filaments and large globose anthers, Dugout Gulch, OR, UF 10417, $\times 1.6$. 13. Similar specimen showing common origin of stamen filaments, Dugout Gulch, OR, UF 10418, $\times 2.1$. 14. Flower showing thick filaments, ten anthers surrounding an elongated style (S) arising from the compressed, carbonaceous fruit body, Fossil, OR, UF 7036, $\times 2.5$. 15. Fragment of flower showing typical calyx venation and large stamens; source of pollen in Figs. 44, 46, Fossil, OR, UF 8381, $\times 3$. 16. Detail from Fig. 13, showing bifurcation of the stamen filament, $\times 5$. 17. Silicone cast from specimen in Fig. 14, showing transversely septate anthers and stigmatic arms at top of style, $\times 4$. 18. Detached androecium and style with five stigmatic arms and five stamens, source of pollen in Figs. 43, 45, 47, 51, 52, UF 8382, $\times 3$. 19. Laterally compressed specimen showing pedicel, androgynophore, and radiating venation of the calyx, UF 10411, $\times 3$. 20. Impression showing rounded-pentagonal outline of the androgynophore, radiating venation of the calyx, and, impressed above the level of the calyx, the laterally compressed fruit body, Dugout Gulch, OR, UF 11745, $\times 3$. 21. Silicone cast of the base of a matured flower, with circular outline representing impression of the base of the fruit, and inner rounded pentagonal outline corresponding to the androgynophore. Note that veins of the calyx radiate from the pedicel scar, Cove Creek, OR, UF 10419, $\times 3$. 22. Silicone cast of the counterpart of the same impression fossil as in Fig. 21, presenting apical view of fruit, showing rounded pentagonal morphology indicative of five carpels, $\times 3$. Bars = 5 mm.



Figs. 23–32. *Florissantia quilchenensis* (Mathewes & Brooke) comb. nov. from the middle Eocene of Republic, Washington. 23. Group of seven flowers compressed in various orientations, showing long pedicels, SR 87-26-4, $\times 1$. 24. Transversely compressed flower showing large gamosepalous calyx and inner whorl of free petals, UWBM 57558, loc. B2737, $\times 1.5$. 25. Transversely compressed pentagonal calyx with laterally compressed elliptical ovary, UWBM 57556, loc. A0307, $\times 1.5$. 26. Detail of petals from Fig. 24, $\times 7.5$. 27. Flower showing pedicel, calyx and stamens, UWBM 56529A, loc. B2737, $\times 1.5$. 28. Detail of flowers from Fig. 23, $\times 1.5$. 29. Laterally compressed flower from Fig. 23, showing pedicel and profile of calyx surrounding the androgynophore, $\times 1.5$. 30. Laterally compressed flower from Fig. 23, showing shallow campanulate morphology, with two stamens exposed, $\times 1.5$. 31. Counterpart of specimen in Fig. 27, showing petals (P), stamens, and elongate style (S), $\times 3.5$. 32. Stamens of the flower in Fig. 30, $\times 4$. Bars = 10 mm in Figs. 23–25, 27–30; 5 mm in Figs. 26, 31, 32.



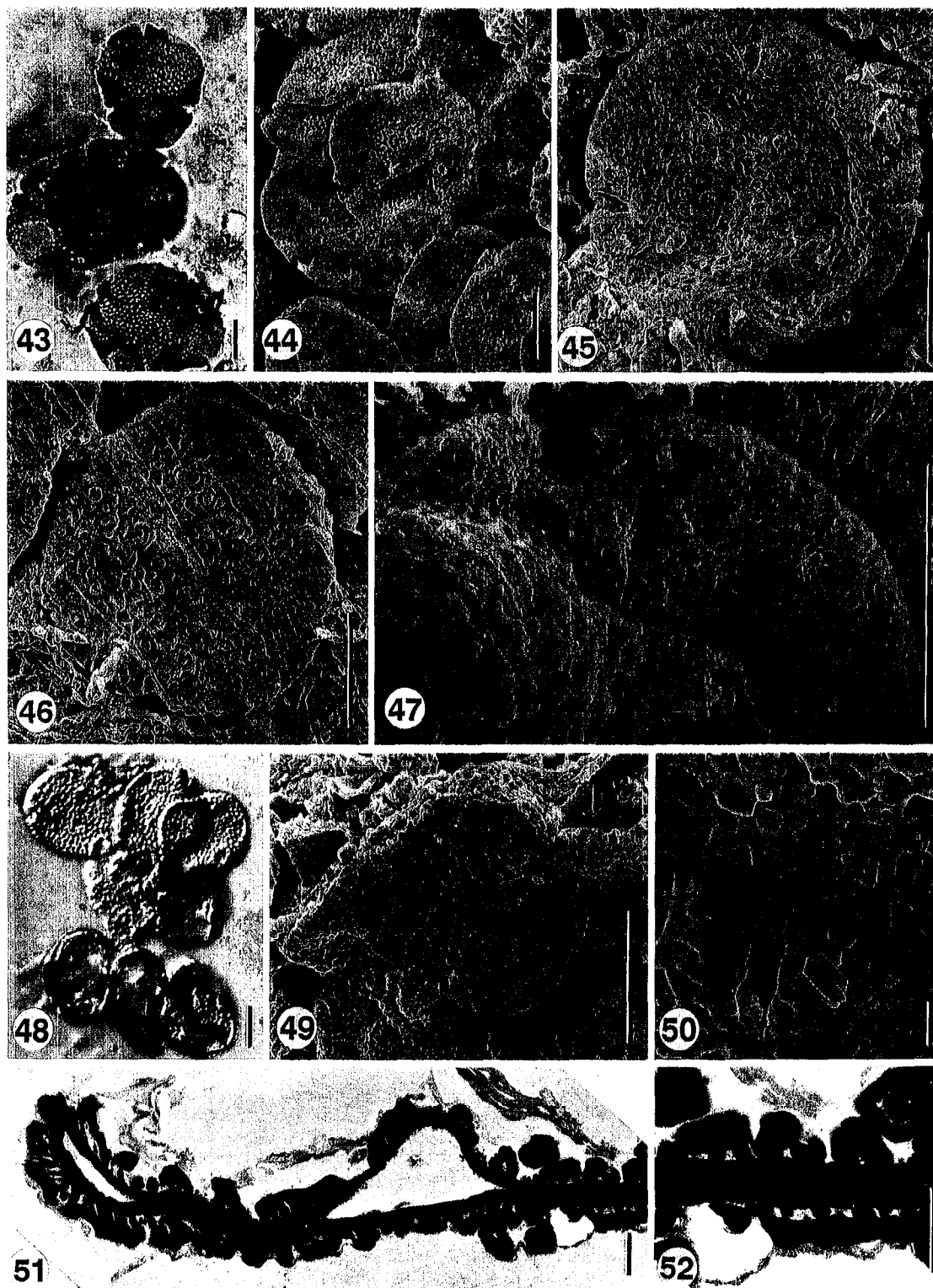
Figs. 33–42. Flowers of *Florissantia ashwillii* sp. nov. from the late Eocene to early Oligocene of Oregon. Figs. 33–38. Typical calyxes, $\times 1.5$. 33. Specimen showing darkened central area in the region of dense hairs of the nectary, UCMP 278. 34. Specimen with well-preserved venation and androgynophore along with typical well-developed calyx lobes, UF 11741a. 35. Flower with three of the stamens exposed, one with an intact anther, UF 11740. 36. Transversely compressed calyx showing perfect symmetry and deep sinuses between lobes, UF 11743. 37. Specimen with rounded, five-ridged fruit body exposed in the center, UF 11749a. 38. Obliquely compressed calyx, showing shallowly concave basal portion, UF 11742a. 39. Counterpart of the specimen in Fig. 38, magnified to show numerous hairs lining basal part of the calyx, probably nectariferous, UF 11742b, $\times 7.5$. 40. Detail of stamens from Fig. 35, showing the continuity of filament bases, $\times 3$. 41. Flower showing the bases of five stamen filaments united into a ring that is semicircular, evidently having ruptured with enlargement of the fruit body, UF 11739, $\times 4.8$. 42. Laterally compressed androecium arising from the faint remains of the calyx, showing five filaments, UF 11744, $\times 3$. Localities: Fig. 33 from Goshen, Oregon. Figs. 34, 35, 37–40 from Sheep Rock Creek. Figs. 36, 42 from Sumner Spring, Oregon. Bars = 10 mm in Figs. 33–38; 5 mm in Figs. 39–42.

flowers. Androgynophore short, expanded to a circular flange at base of the ovary. Ovary superior, pentasyncarpous, with a single style exerted beyond the stamens, and five short stigmatic arms. Androecium of five stamens connate basally into a sleeve around the ovary; filaments often bifurcate once apically; anthers large and globose or elongate, transversely septate. Pollen, when preserved, oblate, tri- and tetracolporate, isopolar, 20–32 μm equa-

torial diam, with short colpi, amb circular to rounded-triangular or squarish, exine reticulate with small lumina decreasing in size toward the equator.

Key to species —

1. Sinuses between calyx lobes shallowly incised (35% or less), calyxes 19–54 mm diam; petals present or absent; anthers globose or elongate.



Figs. 43–52. Pollen from the stamens of *Florissantia* flowers from the Lower Oligocene and Upper Eocene of north central Oregon. Figs. 43–47. *F. speirii* (Lesquereux) comb. nov. from Fossil, Oregon. 43. Pollen from an anther of the androecium in Fig. 18, Tri- and tetracolporate grains, showing thickening of the wall adjacent to the colpi, reticulate exine, transmitted light, UF 8382, $\times 600$. 44. Mass of pollen from anther in Fig. 15 showing nearly orbicular amb of grains, tricolpate, reticulate grains, UF 8381, $\times 1,000$. 45. Detail of tetracolpate grain showing decreased size of lumina of the reticulum toward the equator, UF 8382, $\times 2,000$. 46. Detail of tricolpate grain, UF 8381, $\times 2,000$. 47. Detail of apertural region, UF 8382, $\times 4,000$. Figs. 48–50. *F. ashwillii* from Sheep Rock Creek, Oregon. 48. Mass of pollen from the anther seen in Fig. 35, showing smaller size, relative to Fig. 43, light microscopy, $\times 600$. 49. Pollen from the anther in Fig. 35, showing reticulate surface. SEM, $\times 2,000$. 50. Detail of reticulate exine and colpous. SEM, $\times 6,500$. Figs. 51, 52. *F. speirii*, pollen from flower in Fig. 18. 51. Pollen wall showing continuous foot layer, and collumelae supporting the perforate tectum, UF 8382, TEM, $\times 6,500$. 52. Same, more highly magnified. UF 8382, TEM, $\times 13,000$. Bars = 10 μm in Figs. 43–49; 1 μm in Figs. 50–52.

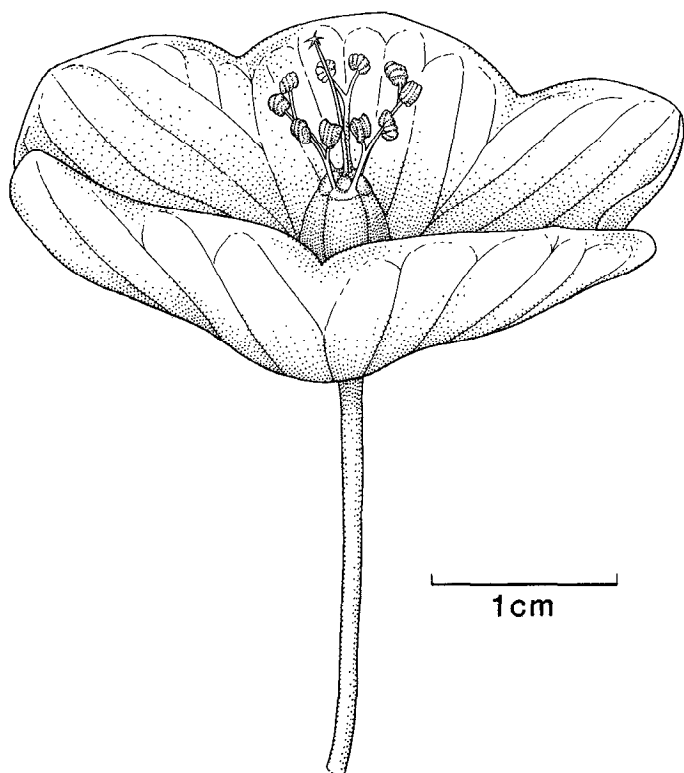


Fig. 53. Reconstruction of *Florissantia speirii* (Lesquereux) new comb., showing the gamosepalous calyx, pentagonal gynoeceum, single style with five stigmatic arms, and the androecium with five bifurcate filaments and ten anthers or half anthers. Illustration by Wendy Zomlefer.

A. Petals absent; anthers globose; calyx 23–54 mm diam

B. Small petals present; anthers elongate; calyx 19–33 mm diam *F. speirii*

. *F. quilchenensis*

II. Sinuses between calyx lobes deeply incised (35%–60%); petals absent, anthers elongate; calyx 21–31 mm diam *F. ashwillii*

Florissantia speirii (Lesquereux) comb. nov.—Figs. 1–9, 11–22, 43–47, 51–53.

Basionym—*Porana speirii* Lesquereux 1883, p. 172, pl. 28, Fig. 15.

Synonymy—*Porana speirii* Lesquereux, Chaney 1927, p. 134 (Gray Ranch, OR), Brown 1935, p. 583, pl. 69, Fig. 3 (Fossil, WY), Brown 1937, p. 185, pl. 61, Fig. 14 (Fossil, WY), Brown 1940, p. 353, Fig. 12 (Gray Ranch, OR), Convolvulaceous (?) flower, Kirchner 1898, pl. 15, Fig. 2 (Florissant, CO), *Porana similis* Knowlton 1916, p. 288, pl. 27, Figs. 1, 2 (Florissant, CO), *Florissantia physalis* Knowlton 1916, p. 270 (Florissant, CO), Manchester and Meyer 1987, p. 121, Fig. 6N, O (Fossil, OR). *Holmskioldia speirii* (Lesquereux) MacGinitie 1953, p. 156, pl. 74, Figs. 1, 2 (Florissant, CO), Brown 1959, p. 128, pl. 24, Fig. 4 (Shale City near Ashland, OR), Becker 1961, p. 87, pl. 30, Figs. 1–3 (Ruby Basin, MT), Meyer 1973, pl. 30, Figs. 3, 4 (Lyons Flora, OR).

Description—Pedicel 0.6–1.0 mm thick, up to 38 mm long. Calyx 23–54 mm diam, gamosepalous, shallowly campanulate, membranaceous, five-parted; lobes rounded to pointed, with prominent radiating reticulate venation. Calyx incision 20%–35%, with lobes varying from well developed, giving a five-lobed outline, to poorly de-

veloped, giving a pentagonal to nearly orbicular outline. Corolla absent. Androgynophore forming a thick circular to rounded-pentagonal disk 2.4–4.0 mm diam, upon which the ovary is seated. Ovary superior, obovate, rounded to five-angled in transverse view, with a single style about 11 mm long, exerted beyond the stamens, and five short stigmas. Androecium consisting of ten anthers borne on five bifurcate filaments that appear to arise/diverge from the apical $\frac{3}{4}$ of the ovary (i.e., the basal portion of the androecium is a tube fused around the ovary). Filaments 6–7 mm long, with large, globose anthers (2–3 mm long). Pollen oblate, 27–32 μ m (Canada balsam) equatorial diam, isopolar, radially symmetrical, tri- and tetracolporate, with short colpi. Amb circular to rounded-triangular or rounded-quadrangular. Exine 770 nm thick, sexine tectate perforate, tectum ca. 300 nm thick, ornamentation reticulate, with smooth muri and more or less angular lumina 0.4–1.3 μ m diam, decreasing in size outward from the poles. Foot layer 230–280 nm thick. Fruit consisting of the enlarged ovary and the persistent calyx and pedicel. Fruit body longer than wide, with five longitudinal ridges that meet at the apex, pentagonal in transverse view, 8–11 mm diam, 9–12 mm high.

Holotype—USNM 387553, from Florissant, Colorado.

Other specimens—From Florissant: USNM 33685, 34236, UCMP 3619, 3620, UF 9982. From the Bridge Creek flora, Oregon: UF 7031, 7036, 8381, 8382, 10409, 10410, 10417–10419, 11745. From West Branch Creek, Clarno Formation, Oregon: UF 11703, 11704. Approximately 65 specimens were examined.

Discussion—The holotype of *Florissantia speirii* (Fig. 1) shows the characteristic connate five-parted calyx with radiating reticulate venation. This and other specimens from the latest Eocene Florissant flora of Colorado (e.g., Figs. 2–5) provide the basis for recognizing the species at many other localities in western North America. The most informative specimens, providing details of the gynoeceum (Figs. 11, 12, 20–22), androecium (Figs. 12–18), and pollen (Figs. 43–47) are from the Oligocene Bridge Creek flora of the John Day Formation, Oregon. Stratigraphically older examples from middle Eocene localities of the Clarno Formation, Oregon (Figs. 8, 9) also conform in characters of the pedicel, calyx, and gynoeceum, although no specimens with details of the androecium and pollen have been recovered. Other records based on calyces without fertile structures preserved include specimens from the Oligocene Lyons (Meyer, 1973) and Shale City (Brown, 1959) floras of western Oregon and from the late Eocene/early Oligocene Ruby flora of southwestern Montana (Becker, 1961).

The specimens are usually oriented in the sediment such that the flower is compressed transversely, showing the symmetrical outline of the calyx (e.g., Figs. 1, 2, 4, 5, 7), but occasionally they are compressed laterally, showing the long persistent pedicel and the shallowly campanulate form of the calyx (Figs. 3, 6). It has been postulated on the basis of large calyx size and long pedicels that these flowers were borne solitary or in loose inflorescences (MacGinitie, 1953). The calyx outline and venation is convergent with that of the extant *Schoutenia* (Tiliaceae, Fig. 10) and *Fryxellia* (Malvaceae), although a close relationship of the fossil to either of these genera is ruled out by differences in other characters. Petals have not

been observed in any specimens of *F. speirii* despite their frequent preservation in specimens of *F. quilchenensis*.

The calyx typically has well-developed, broad lobes with shallow, well-defined sinuses (Figs. 1–3, 5–8), but varies to having more angular lobes and poorly developed sinuses, resulting in a pentagonal calyx outline (Figs. 4, 9). This variability in form of the calyx accounts for the various taxonomic assignments proposed for different specimens of the flower during early investigations of the Florissant flora (Knowlton, 1916). Indeed, the name *Florissantia* was first coined by Knowlton (1916) for a specimen (Fig. 4) which, on the basis of minor differences in size and outline of the calyx, was considered to be generically distinct from the previously described type of *Porana speirii* Lesquereux (Fig. 1).

Many of the specimens appear to represent flowers that have matured to fruiting stage. When transversely compressed flowers are split apart in the shale, one of the counterpart halves, representing the base of the calyx, shows the pedicel attachment and impression of the androgynophore disk (Figs. 19, 21), while the other counterpart, the apical half, bears the impression of an enlarged ovary or fruit body (Fig. 22). When compressed transversely the fruit body clearly shows the pentagonal outline (Fig. 12); when compressed laterally it shows an elliptical to ovate outline (Figs. 11, 20) with an angular to rounded apex bearing a single style (Figs. 14, 17, 18). None of the fruits shows any evidence of dehiscence. In external form, the fruit body resembles that of *Tilia*, which is also nutlike, pentagonal, and indehiscent. Internal fruit structure is not preserved in these fossils; hence the nature of septation, placentation, and seed characters remains unknown.

The thickened, circular, disklike structure at the top of the pedicel (Figs. 19–21) was initially interpreted as the receptacle. However, the venation of the calyx is impressed over its surface (e.g., Fig. 21), indicating that this structure was sandwiched between the calyx and the base of the ovary. The disk is interpreted to represent a short androgynophore. A thin circular rim at the margin of the disk (Fig. 20) is believed to represent the attachment of the androecial sleeve. The indument of the calyx is not preserved in these specimens. However, in compression specimens, the calyx is usually darker-colored near the center of the flower (Figs. 4, 7, 15), suggesting that this region may have been pubescent as in the other species of *Florissantia*, and possibly was nectariferous.

The androecium is rarely preserved; however, seven specimens with intact stamens were recovered after many years of collecting. The filaments are united by their bases into a sleeve surrounding the ovary. At fruiting stage, the androecium is dislodged by the growth of the ovary, and may be detached and missing (the usual case) or may persist as a cap surrounding the style near the apex of the enlarged ovary (Figs. 12–14). In one example, the androecium and style are preserved as a unit detached from the rest of the flower (Fig. 18). The anthers in *Florissantia speirii* are large and globose. Ten anthers (or half anthers) are evident in the more complete specimens (e.g., Figs. 12–14), but one specimen appears to have only five anthers that are bilobed (Fig. 18). Closer scrutiny shows that the specimens with ten anthers have bifurcated filaments (Figs. 16, 17). In each case there are five filaments arising from the column. Each filament splits once prior to the

attachment of anthers. Thus these structures may be interpreted either as ten stamens with partial fusion into five pairs, or as five stamens with half anthers. I was unable to determine from the compressed anthers whether they are monothechal or dithechal. The anther impressions show approximately ten transverse lines interpreted as septations of the type recorded for *Fremontodendron* (van Heel, 1966).

Pollen is preserved in the anthers of only two specimens (Figs. 15, 18). The pollen grains are mostly compressed in the equatorial plane, indicating that the grains were shorter than wide, i.e., oblate. Light microscopy shows that the pollen wall thickens slightly in the region of the pores (Fig. 43). Both tricolporate and tetracolporate grains may occur in the same anther. The exine is reticulate with muri decreasing in size toward the equator (Figs. 44–50). TEM shows tectate columellate exine with moderately well-developed columellae with simple perforations in the tectum (Figs. 51, 52).

Florissantia quilchenensis (Mathewes & Brooke) comb. nov.—Figs. 23–32.

Basionym—*Holmskioldia quilchenensis* Mathewes & Brooke 1971, p. 215, Figs. 15, 16 (Quilchena, British Columbia).

Porana speirii auct. non Lesquereux, Brown, 1935, p. 583, pl. 69, Figs. 1–3 (Green River Formation, WY; Republic, WA), Brown, 1937, p. 185, pl. 61, Fig. 14. *Hydrangea bendirei* auct. non Knowlton, Berry, 1929, p. 251, pl. 52, Fig. 7 (Republic, WA).

Description—Pedicel 0.5–0.7 mm thick, 16–21 mm long. Calyx 19–33 mm diam, gamosepalous, shallowly campanulate, membranaceous, five-parted; calyx incision (0–)17%–33% with lobes varying from well-developed, giving a five-lobed outline, to poorly developed giving a pentagonal to nearly orbicular outline, with prominent radiating reticulate venation; narrowed basally, conforming to the androgynophore. Corolla of five free obovate petals ca. 3.0 mm wide, 3.5 mm long. Petals thick-textured, with prominent subparallel, reticulate venation; alternate with the calyx lobes. Androgynophore up to 2–3 mm long, thickened into a disk at the base of the ovary. Ovary superior, obovate, rounded to five-angled in transverse view, with a single style and five-lobed stigma. Style 8 mm long, exserted beyond the stamens. Androecium consisting of ten stamens on filaments 4–5 mm long. Anthers large, 2–3 mm long, curved. Fruit consisting of the enlarged ovary, persistent calyx, corolla, and pedicel. Fruit body longer than wide, with five longitudinal ridges that meet at the apex, circular to pentagonal in transverse view, 3.5–5.0 mm diam, 5.0–6.0 mm high.

Holotype—SFU Q-97 from Quilchena, British Columbia.

Other specimens—From Republic: UWBM 57556, 57558, 56529, SR87-26-4. Approximately 135 specimens were examined.

Discussion—This species, initially established on the basis of a specimen from the Eocene of Quilchena, southern British Columbia, was initially segregated from *F. speirii* on the basis of having calyx lobes that are poorly developed to “wholly connate, orbicular with no visible lobation” (Mathewes and Brooke, 1971). However, this feature shows considerable overlap between the two spe-

cies when larger collections are taken into consideration. Material that I believe to be conspecific from the Republic flora of northeastern Washington provides additional characters that distinguish the species from *F. speirii*. Calyces of *F. quilchenensis* tend to be smaller than those of *F. speirii* (19–33, vs. 23–54 mm). The most striking difference is the presence of petals in *F. quilchenensis*.

Several specimens show a whorl of five small free petals in addition to the more prominent fused calyx (e.g., Figs. 24, 26, 27, 31). Casual observation might suggest that the smaller, thick-textured structures represent sepals. However, careful study of part and counterpart impressions reveals that the small tepals are positioned in the sediment at a level between the large perianth whorl and the base of the gynoecium. This position indicates that they represent the corolla, while the large whorl represents the calyx. The absence of some or all of the petals in many of the fossils suggests that they were caducous, whereas the calyx clearly was persistent at fruiting stage. The presence of petals distinguishes this species from *F. speirii* and *F. ashwillii*. The large size of the calyx relative to that of the corolla is taken as an indication that these specimens represent fruits in which the calyx was accrescent, having enlarged more than the petals as a function of fruit formation.

Another character distinguishing *F. quilchenensis* from *F. speirii* is the development of an elongate stipe. In laterally compressed specimens, the stipe is evidenced by the narrow shank between the base of the perianth and the base of the ovary (Fig. 29). In transversely compressed calyces there is often a circular torn area in the center where the shale has broken across the neck of the stipe. Some specimens preserve numerous hairs impressed near the base of the calyx, comparable to those that are well-preserved in specimens of *F. ashwillii* (Fig. 39).

Only three specimens are known with stamens preserved. The most complete (Figs. 27, 31) shows approximately ten anthers (or half anthers?). The anthers of *F. quilchenensis* are elongate, rather than globose as those of *F. speirii*. Preservation is not good enough to determine if the anthers are septate, or whether the filaments are bifurcate, as in *F. speirii*, and attempts to retrieve pollen from the anthers were unsuccessful.

Florissantia ashwillii sp. nov.—Figs. 33–42, 48–50.

Description—Pedicel 0.6 mm thick, at least 13 mm long. Calyx 21–31 mm diam, gamosepalous, shallowly campanulate, membranaceous, five-parted; calyx incision 40%–60% with lobes well developed, persistent in fruit, with prominent radiating reticulate venation; narrowed and conforming to outline of androgynophore at base. Petals absent. Androgynophore up to 1.5 mm long, thickened into a disk 1.5–1.7 mm diam at the base of the ovary. Ovary superior, obovate, rounded to five-angled in transverse view, with a single style. Androecium consisting of five stamens with filaments fused by their bases into a narrow circular sleeve around the base of the ovary. Filaments 3.5–6.4 mm long. Anther 1.0 mm wide, 1.9 mm long, elongate, transversely septate. Pollen oblate, 20–22.5 μm (Canada balsam) or 25–27.5 μm (glycerine jelly) equatorial diam, isopolar, radially symmetrical, tricolporate, with short colpi. Amb circular to rounded-triangular. Each aperture situated midway between two adjacent angles in

grains with rounded-angular amb. Ornamentation reticulate, with smooth muri and more or less angular lumina 0.4–1.0 μm . Fruit consisting of the enlarged ovary, the persistent calyx, and pedicel. Fruit body circular to pentagonal in transverse view 4.1–5.6 mm diam, elliptical in longitudinal view.

Holotype—UF 11740, from Sheep Rock Creek, Oregon.

Other specimens—From Sheep Rock Creek: UF 11739, 11741, 11742, 11749. From Sumner Spring, Gray Butte, Oregon: UF 11743, 11744. From the Goshen flora, western Oregon: UCMP 278. Approximately 45 specimens were examined.

Nomenclature—This species was first described, along with a leaf from the Goshen flora of Oregon, as *Viburnum palmatum* Chaney and Sanborn (1933). The leaf specimen, which was designated the holotype, actually appears to be platanaceous and is clearly unrelated to the flower. Although the flower that Chaney and Sanborn illustrated (1933, pl. 40, Fig. 4) was printed without an indication of magnification, it is actually magnified $\times 2$, giving the false initial impression that it is similar in size to typical flowers of *F. speirii*. The specimen (Fig. 33) conforms to the emended diagnosis of *Florissantia*, and is now named as a new species, *F. ashwillii*, in honor of Melvin S. Ashwill, who has provided many of the best specimens of this species.

Discussion—*Florissantia ashwillii* differs from the other two species by its smaller size and more pronounced lobing of the calyx. The percent lobe incision, comparing the radius of the calyx measured to the tip of a lobe with the radius of the calyx measured to the base of a sinus, is 40%–60% in *F. ashwillii* and only 20%–35% in *F. speirii*. Despite excellent preservation, none of the specimens shows any evidence of petals. The absence of petals readily distinguishes the species from *F. quilchenensis*. Some of the specimens preserve numerous, apparently simple, hairs arising from the calyx near the base (Fig. 39). Such hairs occur in extant taxa of Malvales and function as nectaries.

Three specimens have portions of the androecium preserved and reveal that the flower had five stamens. The filaments are thick, apparently unbranched, and are united by their bases into a ring surrounding the ovary (Fig. 41). Although many of the filaments were truncated prior to deposition (Figs. 40, 41), some are more complete (Fig. 42), and one stamen of the holotype is complete with an elongate anther (Figs. 35, 40). This anther shows transverse striations interpreted as septae like those in *F. speirii*, and yielded well-preserved pollen (Figs. 48–50). The pollen is morphologically the same as that from *F. speirii* flowers from Fossil, Oregon, but the grains are considerably smaller.

AFFINITIES

A typical fruit of *Florissantia*, with the persistent membranous calyx and adhering androecium, is reconstructed in Fig. 53 based on the best understood species, *F. speirii*. Similar reconstructions would apply to the other species of *Florissantia*; however, an illustration of *F. quilchenensis* would need to show the set of small free petals arising from the base of the ovary (Fig. 24). The vegetative organs of *Florissantia* are still not known. Although there should be a malvalean leaf type consistently associated with these

fruits at the many different localities, I have not been successful in identifying a suitable candidate.

The floral and pollen morphology of *Florissantia* provides ample justification for placement of the genus within the Malvales. Malvacean characters of the flowers include actinomorphy, hypogyny, bisexual flowers, basally connate calyx, free or absent petals, dense indumentum at base of perianth, presence of an androgynophore, pentamerism of calyx, corolla, carpels, and stamens, a single style, and filaments united basally into a tube around the ovary, as well as brevicolporate, reticulate pollen. These characters are shared among various genera of Tiliaceae, Malvaceae, Bombacaceae, and Sterculiaceae; however, the precise combination of characters found in *Florissantia* does not occur in any single extant genus.

Because of overlap in many morphological characters between Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae, the familial position of *Florissantia* is not immediately obvious. These families are much in need of reevaluation with modern methods of phylogenetic analyses, and it might be more logical to merge them into one family, on the grounds that only the Sterculiaceae tribe can be distinguished by unique derived characters (W. Judd, personal communication, 1991). For purposes of this discussion, I accept the traditional treatment of these families (Engler, 1964; Hutchinson, 1967; Cronquist, 1981). Some of the more distinctive features of *Florissantia* occur in more than one of these families. For example, bifurcate stamen filaments occur in Malvaceae, Bombacaceae, and sometimes Tiliaceae (e.g., *Tilia*). Oblate pollen with apertures situated between the angles of the grain occur in Bombacaceae, Sterculiaceae, and Tiliaceae. Petals may be reduced or absent in each of these families. However, by a rather cumbersome process of elimination, *Florissantia* can be attributed to the Sterculiaceae.

Although showy actinomorphic flowers and bifurcate stamen filaments bring to mind Malvaceae, *Florissantia* is distinguished from the Malvaceae in various characters. The Malvaceae usually have numerous or very numerous stamens (but sometimes only five), with filaments all connate into a tube for most of their length, and have monothecal anthers. The fruits are generally dehiscent (schizocarps and capsules) or baccate, but dry indehiscent fruits of the type in *Florissantia* are atypical among extant Malvaceae. The spinose, usually spheroidal pollen characteristic of most Malvaceae (Erdtman, 1952; Christensen, 1986) is unlike that of *Florissantia*.

Florissantia can be distinguished with some confidence from the Tiliaceae on the basis of stamen characters. Flowers of Tiliaceae typically have numerous stamens (rather than just five or ten), and the anthers are usually small, less than 0.5 mm (although *Luehea* stamens are > 1 mm). Extant *Schoutenia* closely parallels *Florissantia* in possessing a large, membranous, shallowly campanulate calyx that is persistent in fruit (Fig. 10). However, *Schoutenia* differs in several important characters, including the rounded rather than pentangular fruit body, the numerous stamens with small anthers (Hartono, 1965), and spiny pollen (Sharma, 1969). Pollen that is at least superficially similar to that of *Florissantia*, i.e., tri-brevicolporate, peroblate to suboblate, and appearing by light microscopy to be reticulate or microreticulate, occurs in several genera of Tiliaceae and is referred to as the *Tilia*

type by Erdtman (1952). However, Praglowski (1971) and Christensen and Blackmore (1988) demonstrated that the tectum of *Tilia* is not truly reticulate; rather, it is actually continuous with funnel-like surface cavities situated over infratectal baculae. This trait, referred to as "*Tilia*-structure" (Christensen and Blackmore, 1988), differs from the truly reticulate structure of *Florissantia* pollen, and might serve to distinguish the fossils from other Tiliaceae as well. What appears to be similar structure, although not confirmed by TEM studies, is described as semitectate and suprareticulate in *Melochia* (Sterculiaceae; Dorr and Barnett, 1989). Although light micrographic surveys of extant tiliaceous pollen have been published (Erdtman, 1952; Sharma, 1969), thorough electron micrographic investigations are not yet available for most tiliaceous genera.

Eliminating Malvaceae and Tiliaceae by the above criteria, the Bombacaceae and Sterculiaceae remain as candidates for the placement of *Florissantia*. The number of locules per anther has been used as a key character distinguishing Sterculiaceae (dithecal) and Bombacaceae (monothecal), although there is some overlap in this feature. However, it was not possible to observe the number of thecae per anther in the compressed fossil remains. In *F. speirii* and *F. ashwillii*, where preservation is sufficiently good to assess anther structure, it appears that the anthers possess transverse septa (Fig. 17), a feature peculiar to *Nesogordonia* (cited as *Cistanthera*, van Heel, 1966) and *Fremontodendron* in the Sterculiaceae (van Heel, 1966) and to *Phragmotheca*, *Septotheca*, and *Huberodendron* in the Bombacaceae (Hutchinson, 1967; Alverson, 1991). In the number of stamens as well as the transversely septate stamens, *Florissantia* resembles *Fremontodendron*, a genus that has been placed by different authors both in Sterculiaceae and in Bombacaceae (Kelman, 1991); however, these genera differ significantly in perianth development.

Pollen like that of *Florissantia* (Figs. 43–52) with the combined characters of oblate shape, reticulate exine, and short colpi that are situated between the angles of the grain is characteristic of some Sterculiaceae (*Chiranthodendron*, *Fremontodendron*, *Leptonychia*, *Mansonia*) and some Bombacaceae (*Bombax*, *Eriotheca*, *Pseudobombax*) (Erdtman, 1952; Fuchs, 1967; Nilsson and Robyns, 1986). Based on the comprehensive survey of extant bombacaceous pollen by Nilsson and Robyns (1986), pollen of *Florissantia* conforms to the "*Bombax*-subtype" of the "*Bombax*-type" sensu Nilsson and Robyns. However the fossil pollen, measuring 20–32 μm in equatorial diam, is considerably smaller than pollen of most extant Bombacaceae, which usually falls within the range of 50 to 100 μm (Nilsson and Robyns, 1986). Because a detailed palynological survey of the Sterculiaceae is not yet available, it is difficult to assess the level of similarity between *Florissantia* pollen and that of extant Sterculiaceae; however, many genera in this family have pollen within the size range of *Florissantia* (Erdtman, 1952).

Whereas flowers of Bombacaceae are usually very large, accommodating bird and bat pollination, those of Sterculiaceae are typically small to medium-sized and are commonly insect-pollinated. There are exceptions to this generalization; for example, the relatively large flowers of *Pterospermum* (Sterculiaceae). However, flowers of *Flor-*

issantia are small in relation to those of most Bombacaceae, and by the size criterion are more similar to those of Sterculiaceae.

Aside from the character of anther locule number, which admittedly overlaps to some extent between Sterculiaceae and Bombacaceae (Cronquist, 1981), there is no clear distinction between these families, and one could argue for placement of *Florissantia*, and indeed many extant genera, in either of them. Awaiting a more satisfactory familial classification of extant Malvales, *Florissantia* is tentatively placed in the Sterculiaceae.

POLLINATION AND DISPERSAL

Flowers of *Florissantia* possess a syndrome of characters suggestive of insect and/or bird pollination. The long slender pedicels suggest that the flowers were pendant. The dense pubescence at the base of the calyx probably functioned as a nectary as in many extant malvalean genera. The style and stamen filaments are thick and fibrous, a feature commonly associated with bird- and bat-pollinated flowers (Faegri and van der Pijl, 1979). Although the calyx is of sufficient size to suggest that the flowers were showy, it is important to recognize that most of the fossils represent flowers that had reached fruiting stage. The calyx may have been accrescent, reaching full size after anthesis, in connection with fruit development. This might explain why the calyx extends well beyond the petals in specimens of *F. quilchenensis*. If the petal spread in these specimens is taken as an indication of original flower size, then the diameter was about 6 to 8 mm. Differences in perianth configuration and stamen size among the species of *Florissantia* might reflect divergent modes of pollination, involving different species of insects and/or birds.

Functionally, the fruits of *Florissantia* may be described as samaras with the persistent calyx forming a wing around the matured ovary. None of the fossils show the fruit body in a dehiscent condition, and the fruits were evidently indehiscent. Wind-dispersal was probably a major factor in distributing *Florissantia* fruits, as may be inferred from the abundance of these samaras in lake deposits where other kinds of fruits are rare.

EVOLUTIONARY CONSIDERATIONS

Among extant Malvales, there is a spectrum in androecial development from numerous free stamens, to stamens in fascicles, to monadelphous stamens (van Heel, 1966). If it is correct to assume that numerous free stamens are primitive for the Malvales, as suggested by taking Theales as an outgroup, then the presence of only five or ten stamens in *Florissantia* indicates reduction. The relatively large stamens of *F. speirii*, and the septate anthers, also are probably derived features that may be related to mode of pollination.

Although the fossil record of insect pollination in angiosperms is becoming increasingly well documented (Crepet, Friis, and Nixon, 1991), that of bird and bat pollination has received very little attention. Extant Bombacaceae include many species with large flowers that are pollinated by birds and many that are pollinated by bats (Faegri and van der Pijl, 1979; Alverson, 1989). *Floris-*

santia, with its small to medium-sized nectariferous flowers, lax pedicels, and strong stamen filaments, may signify a trend from insect pollination, common in many Sterculiaceae, toward the bird and bat pollination syndromes that were important in the evolution of extant genera of Bombacaceae.

DISTRIBUTION

Florissantia typically occurs in tuffaceous lake-deposited shales, so it is likely that the genus was an important element of lakeside vegetation, particularly in volcanic areas. It is only known from western North America, and its absence from other well-collected Tertiary floras in the Northern Hemisphere is conspicuous. *Florissantia* spanned approximately 15 MY, extending from the middle Eocene to the early Oligocene, and ranged considerably in latitude and elevation. The most northerly occurrence is based on an incomplete specimen from the Oligocene of southern Alaska ("*Holmskioldia speirii* [Lesq.] MacG?" in Wolfe, 1977). *Florissantia* is well represented in the middle Eocene by specimens of *F. quilchenensis* from the Quilchena and Princeton floras of southern British Columbia and from the Republic flora in northeastern Washington, and by specimens of *F. speirii* from the Clarno Formation in north central Oregon. The genus extended from coastal areas of western Oregon as far inland as central Colorado. *F. speirii* spans the Eocene/Oligocene boundary, extending from subtropical/tropical vegetation of the Clarno flora to temperate vegetation of the Bridge Creek flora. Some of the localities, such as the Lyons flora of western Oregon, were probably within 200 m of sea level, whereas the paleoaltitude of *Florissant* has been estimated at about 2,450 m (Meyer, 1986).

REAPPRAISAL OF THE FOSSIL RECORD OF VERBENACEAE

The Verbenaceae, mainly a Southern Hemisphere family, were previously considered to be present in the early Tertiary of North America (Taylor, 1990) on the basis of fossils identified as flowers of *Petrea* and *Holmskioldia* from the Florissant beds of Colorado (MacGinitie, 1953) and leaf impressions attributed to *Clerodendrum* sp. from the Eocene of Alaska (Wolfe, 1977). The flowers that were assigned to *Holmskioldia* are now transferred to *Floris-santia* in the Malvales, and the specimens described as flowers of *Petrea perplexans* (Cockerell) MacGinitie (1953) have been shown to be fruits of an extinct genus of Betulaceae (Manchester and Crane, 1987). As a result, there is currently no unequivocal support for recognition of Verbenaceae in the Tertiary of North America.

LITERATURE CITED

- ALVERSON, W. S. 1989. *Quararibea* (Bombacaceae): five new species from moist and wet forests of Costa Rica and Panama. *Brittonia* 41: 61-74.
- . 1991. A synopsis of *Phragmothea* (Bombacaceae), with two new species and a new subspecies. *Brittonia* 43: 73-87.
- ASHWILL, M. S. 1983. Seven fossil floras in the rain shadow of the Cascade Mountains, Oregon. *Oregon Geology* 45: 107-111.
- BECKER, H. F. 1961. Oligocene plants from the upper Ruby River basin, southwestern Montana. *Geological Society of America Memoir* 82: 1-127.

- BERRY, E. W. 1929. A revision of the flora of the Latah Formation. *U.S. Geological Survey Professional Paper* 154-H: 225-265, pls. 49-64.
- BROWN, R. W. 1935. Miocene leaves, fruits, and seeds from Idaho, Oregon, and Washington. *Journal of Paleontology* 9: 572-587.
- . 1937. Additions to some fossil floras of the western United States. *U.S. Geological Survey Professional Paper* 186-J: 163-206, pls. 45-63.
- . 1940. New species and changes of name in some American fossil floras. *Journal of the Washington Academy of Sciences* 30: 344-356.
- . 1959. A bat and some plants from the upper Oligocene of Oregon. *Journal of Paleontology* 33: 125-129, pl. 24.
- BŮŽEK, C., KVAČEK, Z., AND S. R. MANCHESTER. 1989. Sapindaceous affinities of the *Pteleacarpum* fruits from the Tertiary of Eurasia and North America. *Botanical Gazette* 150: 477-489.
- CHANEY, R. W. 1927. Geology and palaeontology of the Crooked River Basin, with special reference to the Bridge Creek flora. *Carnegie Institution of Washington Publication* 346: 45-138, pls. 8-20.
- , AND E. I. SANBORN. 1933. The Goshen flora of west central Oregon. *Carnegie Institution of Washington Publication* 439: 1-103, pls. 1-40.
- CHRISTENSEN, P. B. 1986. Pollen morphological studies in the Malvaceae. *Grana* 25: 95-117.
- , AND S. BLACKMORE. 1988. The Northwest European pollen flora, 40. Tiliaceae. *Review of Palaeobotany and Palynology* 57: 33-43.
- CREPET, W. L., E. M. FRIIS, AND K. C. NIXON. 1991. Fossil evidence for the evolution of biotic pollination. *Philosophical Transactions of the Royal Society of London B* 333: 187-195.
- CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, NY. 1,262 pp.
- DORR, L. J., AND L. C. BARNETT. 1989. A revision of *Melochia* section *Physodium* (Sterculiaceae) from Mexico. *Brittonia* 41: 404-423.
- ENGLER, A. 1964. *Syllabus der Pflanzenfamilien*, vol. 2. Gebrüder Borntraeger, Berlin. 666 pp.
- EPIS, R. C., AND C. E. CHAPIN. 1974. Stratigraphic nomenclature of the thirty-nine mile volcanic field, central Colorado. *Bulletin of the U.S. Geological Survey* 1395-C: 1-23.
- ERDTMAN, G. 1952. Pollen morphology and plant taxonomy angiosperms. Almquist and Wiksel, Stockholm. Reprinted 1986 by E. J. Brill, Leiden. 553 pp.
- FAEGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination ecology, 3d ed. Pergamon, Oxford.
- FUCHS, H. P. 1967. Pollen morphology of the family Bombacaceae. *Review of Palaeobotany and Palynology* 3: 119-132.
- HALL, J. W., AND A. M. SWAIN. 1971. Pedunculate bracts of *Tilia* from the Tertiary of western United States. *Bulletin of the Torrey Botanical Club* 98: 95-100.
- HARTONO, R. 1965. A monograph of the genus *Schoutenia* Korth. (Tiliaceae). *Reinwardtia* 7: 91-138.
- HUTCHINSON, J. 1967. The genera of flowering plants, vol. 2. Clarendon Press, Oxford. 659 pp.
- KELMAN, W. M. 1991. A revision of *Fremontodendron* (Sterculiaceae). *Systematic Botany* 16: 2-20.
- KIRCHNER, W. C. G. 1898. Contribution to the fossil flora of Florissant, Colorado. *Transactions of the St. Louis Academy of Science* 8: 161-188, pls. 11-15.
- KNOWLTON, F. H. 1916. A review of the fossil plants in the United States National Museum from the Florissant lake beds at Florissant, Colo., with descriptions of new species and list of type specimens. *Proceedings of the U.S. National Museum* 51: 241-297.
- KRÜTZSCH, W. 1970. *Reevesiapolis*, ein neues Pollengenus der Sterculiaceen aus dem mitteleuropäischen Tertiär. *Feddes Repertorium* 81: 371-384.
- KVAČEK, Z., C. BŮŽEK, AND S. R. MANCHESTER. 1991. Fossil fruits of *Pteleacarpum* Weyland—Tiliaceous, not Sapindaceous. *Botanical Gazette* 154: 522-523.
- LESQUEREUX, L. 1883. Contributions to the fossil flora of the western Territories, part 3, the Cretaceous and Tertiary floras. *Report of the U.S. Geological Survey of the Territories* 8: 1-283.
- MACGINITIE, H. D. 1953. Fossil plants of the Florissant beds, Colorado. *Carnegie Institution of Washington Publication* 599: 1-198.
- MAI, D. H. 1961. Über eine fossile Tiliaceen-Blüte und tilioide Pollen aus dem deutschen Tertiär. *Geologie* 10: 54-93.
- MANCHESTER, S. R. 1979. *Triplochitoxylon* (Sterculiaceae): a new genus of wood from the Eocene of Oregon and its bearing on xylem evolution of the extant genus *Triplochiton*. *American Journal of Botany* 66: 699-708.
- . 1980. *Chattawaya* (Sterculiaceae): a new genus of wood from the Eocene of Oregon and its implications for xylem evolution of the extant genus *Pterospermum*. *American Journal of Botany* 67: 59-67.
- . 1990. Eocene to Oligocene floristic changes recorded in the Clarno and John Day Formations, Oregon, USA. In E. Knobloch and Z. Kvaček [eds.], *Proceedings of the symposium on paleofloristic and paleoclimatic changes in the Cretaceous and Tertiary*, 183-187. Geological Survey Publisher, Prague.
- . 1991. Fossil record and evolution of *Tilia* fruiting bracts. *American Journal of Botany* 78: 119 (Supplement).
- , AND P. R. CRANE. 1987. A new genus of Betulaceae from the Oligocene of western North America. *Botanical Gazette* 148: 263-273.
- , AND H. W. MEYER. 1987. Oligocene fossil plants of the John Day Formation, Fossil, Oregon. *Oregon Geology* 49: 115-127.
- , AND R. B. MILLER. 1978. Tile cells and their occurrence in Malvacean fossil woods. *IAWA Bulletin* 1978/2-3: 23-28.
- MATHEWES, R. W., AND R. C. BROOKE. 1971. Fossil Taxodiaceae and new angiosperm macrofossils from Quilchena, British Columbia. *Syesis* 4: 209-216.
- MCFADDEN, J. J. 1986. Fossil flora near Gray Butte, Jefferson County, Oregon. *Oregon Geology* 48: 51-55, 58.
- METCALFE, C. R., AND L. CHALK. 1950. *Anatomy of the dicotyledons*, vols. 1, 2. Clarendon Press, Oxford.
- MEYER, H. 1973. The Oligocene Lyons flora of northwestern Oregon: Oregon Department of Geology and Mineral Industries. *Ore Bin* 35: 37-51.
- . 1986. An evaluation of the methods for estimating paleoaltitudes using Tertiary floras from the Rio Grande Rift vicinity, New Mexico and Colorado. Ph.D. dissertation, University of California, Berkeley, CA.
- MULLER, J. 1981. Fossil pollen records of extant angiosperms. *The Botanical Review* 47: 1-142.
- NILSSON, S., AND A. ROBYNS. 1986. Bombacaceae. *World Pollen and Spore Flora* 14: 1-59.
- PRAGLOWSKI, J. R. 1971. Reticulate and allied exines. *Grana* 11: 79-86.
- SAPORTA, G., DE. 1862. Études sur la végétation du sud-est de la France à l'époque Tertiaire. *Annales des sciences naturelles. Botanique* 17: 191-311, (4th series), pls. 1-14.
- . 1873. Études sur la végétation du sud-est de la France à l'époque Tertiaire. *Annales des sciences naturelles. Botanique* 17: 23-146, (5th series), pl. 6-18.
- SHARMA, B. D. 1969. Pollen morphology of Tiliaceae in relation to plant taxonomy. *Journal of Palynology* 5: 7-29.
- SWISHER, C. C., III, AND D. R. PROTHERO. 1990. Single-crystal ⁴⁰Ar/³⁹Ar dating of the Eocene-Oligocene transition in North America. *Science* 249: 760-762.
- TAYLOR, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and Early Tertiary of the North American area. *The Botanical Review* 56: 297-417.
- VAN HEEL, W. A. 1966. Morphology of the androecium in Malvales. *Blumea* 13: 182-394.
- WHEELER, E. F., M. LEE, AND L. C. MATTEN. 1987. Dicotyledonous woods from the Upper Cretaceous of southern Illinois. *Botanical Journal of the Linnean Society* 95: 77-100.
- WOLFE, J. A. 1977. Paleogene floras from the Gulf of Alaska Region. *U.S. Geological Survey Professional Paper* 997: 1-108.
- . 1989. Leaf-architectural analysis of the Hamamelididae. In P. R. Crane and S. Blackmore [eds.], *Evolution, systematics and fossil history of the Hamamelididae*, 75-104. Oxford University Press, Oxford.
- , AND W. WEHR. 1987. Middle Eocene dicotyledonous plants from Republic, Northeastern Washington. *U.S. Geological Survey Bulletin* 1597: 1-25.